Distribution and Affinities of the Brachyuran Crustacea[1]

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History of Exploration

KNOWLEDGE of the decapod crustaceans, and particularly, of the Brachyura, or short-tailed crabs, of the Baja California-Gulf of California region, goes back barely a century and may be said to date from the early work of John Xantus, who established for the U. S. Coast Survey and maintained, for less than a two-year period, 1859–1861, a tidal gauge station at Cape San Lucas. The specimens that he collected in the immediate vicinity, upon shipment to the U. S. National Museum, became the basis for two fundamental papers by William Stimpson (1860, 1871). A second source were the collections of W. J. Fisher from the Gulf of California and of Henry Edwards from Mazatlán, reported by W. N. Lockington (1877). Regrettably, Stimpson's collections were destroyed in the Chicago fire of 1871, Lockington's in the San Francisco earthquake and fire of 1906. But for the practice of sending syntypes to other institutions, of Stimpson's species to the Museum of Comparative Zoology, Harvard, of Lockington's to the Museum of Natural History, Paris, we would be entirely lacking in specimen material from this early period.

Other collectors who worked either in the littoral or at shallow depths were Verreaux (Saussure, 1853), Diguet (Bouvier, 1895), Orcutt, and Anthony (Rathbun, 1918, 1925, 1930). For the exploration of the deeper waters we are indebted to the U. S. Fish Commission Steamer *Albatross* expeditions of 1887–88 (Rathbun, 1898), of 1891 (Rathbun, 1893), and 1911 (Rathbun, 1923). The modern era of exploration of the Gulf of California may be said to have begun with the California Academy of Sciences expedition in 1921 (Rathbun, 1924) and has been continued by the Templeton Crocker expedition in 1936 (Glassell, 1936; Crane, 1937a, b), and by the Allan Hancock expeditions of 1936, 1937, 1940 (Garth, 1939, 1940), and 1949. Significant contributions have also been made by latter-day independent collectors, among whom should be mentioned H. N. Lowe (Rathbun, 1933), S. A. Glassell (Glassell, 1935), E. F. Ricketts (Steinbeck and Ricketts, 1941), and F. Bonet (Buitendijk, 1950).

The affinities of the brachyuran fauna of the Gulf of California were studied by the late Steve A. Glassell (1934), who noted that "in general it is in the Gulf of California that the tropical species make their most northerly advance on the Pacific coast of North America, although of course some few species have their most northern limits far north of the Gulf." Glassell's study was limited to the brachyuran Crustacea of the three major groups: the cancroid or cyclometopous crabs, the grapsoid or catometopous crabs, and the spider or oxyrhynchous crabs, and was to a large extent a compilation from the literature, in particular, an abstract of information contained in monographs of the late Mary J. Rathbun (grapsoid, 1918; spider, 1925; cancroid, 1930). His personal collecting activities in the Gulf of California and at Magdalena Bay during the 1931–1933 period, however, accounted for 112 species: cancroid crabs 47, grapsoid crabs 32, spider crabs 33, or 56% of the

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recorded fauna. Since specific localities were not given for the 46 new records obtained, 18 of which were introductions to the Gulf of California fauna, it has not been possible to credit Glassell with these by citation of published record. However, his careful compilation has proved useful for purposes of comparison and as a point of departure for subsequent faunistic studies.

Including his own collections, the total number of species of the three groups found by Glassell within the Gulf of California (Cape San Lucas to Mazatlán) and at Magdalena Bay on the west coast of Baja California was 197, divided as follows: cancroid crabs 77, grapsoid crabs 54, spider crabs 66. Panamanian species intruding into the Gulf of California region thus bounded numbered 96: cancroid crabs 39, grapsoid crabs 25, spider crabs 32. Species indigenous to the Gulf of California numbered 75: cancroid crabs 27, grapsoid crabs 22, spider crabs 26. Northern species, on the other hand, numbered only 24: cancroid crabs 11, grapsoid crabs 5, spider crabs 8. To recapitulate, of a total of 195 species (eliminating two of doubtful provenience), 96 species, or 48%, were Panamanian, 75 species, or 40%, were indigenous, and 24, or 12%, were of northern origin.

Expeditions subsequent to 1935 that have added materially to our knowledge of the fauna of the region include the *Zaca* expedition of William Beebe in 1936 (Glassell, 1936; Crane, 1937a), the *Velero III* cruises of 1936, 1937, and 1940 (Garth, 1939, 1940), and the *Velero IV* cruise of 1949 (Garth, 1958). As a result of these expeditions, 10 new species, 4 cancroid, 3 grapsoid, and 3 spider crabs, were described, and another 16 species, 5 cancroid, 2 grapsoid, and 9 spider crabs, were recorded for the first time from the Gulf of California. The publication of the fourth monograph on the oxystomatous and allied crabs of America (Rathbun, 1937), and the appearance of the *Zaca* expedition report on the same group of crustaceans (Crane, 1937b), makes it possible to subject this final segment of the marine Brachyura to the same analysis applied by Glassell to the other three.

While the Brachyura of the Allan Hancock Expeditions in the Gulf of California and along the west coast of Baja California have been the subject of continuing studies, these have been reported only in part. Preliminary descriptions of the oxystomatous and allied crabs appeared (Rathbun, 1935) in advance of their monographic treatment (Rathbun, 1937). Similarly, preliminary descriptions of oxyrhynchous or spider crabs appeared (Garth, 1939, 1940) in advance of their comprehensive treatment (Garth, 1958), together with those of the cancroid or cyclometopous crabs, awaiting treatment. The monograph on the cancroid crabs is sufficiently advanced to permit the use of species and locality data with a reasonable degree of confidence. The status of the grapsoid or catometopous crabs, however, is essentially that in which they were left by Rathbun (1918) and by Glassell (1934).

While Glassell recognized both a northern (Californian) and a southern (Panamic) element in the west coast of Baja California-Gulf of California region, he made no attempt to establish faunal boundaries. This was done by the writer in his studies on the warm-temperate fauna on the west coast of North America (Garth, 1955), who pointed out that the intertidal regions of the Gulf of California, from Agua Verde Bay on the west (peninsular) coast to Puerto San Carlos on the east (mainland) coast, constitute in effect a Pacific Mediterranean region, of which the present communication with the ocean, unlike the Strait of Gibraltar, now lies within the tropics. Furthermore, it was pointed out in studies on the brachyuran fauna of Chile and Peru (Garth, 1957) that this warm-temperate fauna had its counterpart in the southern hemisphere, as shown by the existence of species pairs in genera exhibiting tropical discontinuity. Against this background

we may proceed to consider in some detail the distribution of the Brachyura by major groups on the west coast of Baja California, in the Gulf of California, and in islands to the south.

The West Coast of Baja California

The west coast of Baja California, at least in its northern portion, provides a continuum of habitat for north-temperate species found in the littoral zone of southern California south of Pt. Conception. Rocky shore, sandy beach, and muddy lagoon alternate to provide a variety of ecological situations no less hospitable to cold-adapted species than those found north of the United States–Mexico boundary. This favorable environment for temperate species exists at least as far south as Pta. Eugenio, opposite Cedros Island, and locally as far south as Pta. Entrada, outside Magdalena Bay. Since it is within this area that the temperate and tropical faunas meet and mingle, the progress of the northern, and then of the southern element along this coastline will be considered in some detail.

Of the truly boreal crabs, one group of anomurous forms, the family Lithodidae, deserves mention. These were believed to come no farther south than Monterey in the littoral; the deep-water species, such as *Lopholithodes foraminatus* and *Paralithodes rathbuni,* reached the latitude of San Diego (Schmitt, 1921). Within the last decade, however, *Hapalogaster cavicauda* has been collected intertidally at Laguna Beach by Hancock Foundation parties, at Pta. Santo Tomás by William K. Emerson, and at San Geronimo Island by M. Woodbridge Williams; the last two are Baja California localities.

Among the spider crabs, family Majidae, the truly boreal element, comprising the genera *Oregonia, Hyas,* and *Chionoecetes,* has disappeared from the littoral north of Cape Mendocino, California; however, *C. tanneri* has been dredged from near Tanner Bank, on the Mexican border, in several hundred fathoms. A second group of cold-temperate species, including the decorator crabs, *Scyra acutifrons, Loxorhynchus grandis,* and *L. crispatus,* have their southern limit north of Pta. Eugenio and do not occur in the northern part of the Gulf of California. It is the third group, the warm-temperate species, consisting of *Podochela lobifrons* (formerly known as *P. barbarensis*), *Erileptus spinosus,* and *Pyromaia tuberculata,* that are common to southern California-northern Baja California, and Gulf of California waters.

Of the six Pacific American species of kelp crabs of the genus *Pugettia,* four have their southern terminus of range off Baja California: *P. producta* at Santa Rosalia Bay (or Rosarito Point), *P. richi* at San Geronimo Island, *P. dalli* off Thurloe Head, and *P. venetiae* outside Magdalena Bay, while a fifth, *P. hubbsi,* is a Guadalupe Island endemic species. The giant kelp crab, *Taliepus nuttalli,* occurs in *Macrocystis* beds south to Pta. Entrada. None of the larger kelp crabs occur in the Gulf of California, their place being taken by the smaller sargassum crabs, *Acanthonyx petiveri* and *Epialtus minimus.* The controlling factor is here an ecological one, as the kelps themselves are absent from Gulf of California waters.

Of the nine species of crabs of the genus *Cancer,* family Cancridae, found in the American north Pacific, five have their southern limit of range off Baja California: *Cancer gracilis* at Playa Maria Bay, *C. antennarius* at Todos Santos Island, *C. jordani* at Thurloe Head, *C. anthonyi* at Magdalena Bay, and *C. amphioetus* at Magdalena Bay and also in the Gulf of California.

Of the pebble crabs, family Xanthidae, only the genus *Lophopanopeus* ranges north of Monterey, California. The southern limits of range of its three species (as reduced from five by Menzies, 1948) are as follows: *L. bellus diegensis,* San Diego; *L. leucomanus,* Rosarito Beach; *L. frontalis,* Magdalena Bay (as *L. heathi* Rathbun), and also in the Gulf of Cali-

fornia. In addition to *Lophopanopeus,* three other xanthid genera occur in California (excluding *Rhithropanopeus,* a recent introduction to San Francisco Bay). These are *Cycloxanthops,* with *C. novemdentatus* ranging to Pta. Abreojos, *Paraxanthias,* with *P. taylori* ranging to Magdalena Bay, and *Pilumnus,* with *P. spinohirsutus* ranging to Pta. Entrada, outside Magdalena Bay, and a cognate species, *P. townsendi,* inside Magdalena Bay and in the Gulf of California.

Among the grapsoid crabs of the family Grapsidae, the lined shore crab, *Pachygrapsus crassipes,* has its southern limit at Santa Margarita Island and occurs also in the Gulf of California. The closely related species of *Hemigrapsus, H. nudus* and *H. oregonensis,* have their southern limits at Turtle Bay and Todos Santos Bay (Rathbun, 1923), respectively. The latter, as reported from the Gulf of California by Rathbun (1918), was later determined by her to be a new species, *Goetice americanus* (Rathbun, 1923).

It will have been noted that when a north-temperate genus is represented in the Gulf of California it is by a single species only, and that where this genus is represented by several species on the west coast of Baja California, it is the species with the most southerly terminus of range that occurs in the Gulf of California. This is true in *Cancer* of *C. amphioetus* and in *Lophopanopeus* of *L. frontalis.* It would be true of *Hemigrapsus* if *Goetice americanus* = *Hemigrapsus oregonensis* as originally identified by Rathbun. It is also noticeable that when the Gulf of California range of these species is compared with their west coast of Baja California range, the southern limit in the Gulf of California is almost always farther north than on the open Pacific coast. This corresponds with what is known of temperatures in the region, as the outer coast is under a northerly current regime, with frequent upwelling, while the Gulf of California is cut off from northerly currents, with upwelling and associated phenomena modified by local conditions.

The similarity of the warm-temperate faunas of northern Baja California and of the Gulf of California suggested to the early naturalists past water connections between them. These have been placed variously: at the level of the Magdalena Plain, at the mid-peninsular level below the Sierra Vizcaíno, or above the Sierra Vizcaíno at the level of Scammon Lagoon. While each of these situations can be shown to have existed in the geological past, it is not necessary to go beyond the Pleistocene to explain the present distribution. A slight southward displacement of present-day isotherms, coupled with such rises in sea level as are known to have occurred interglacially, would again unite the warm-temperate faunas of the two regions.

Let us now consider the tropical fauna of this same coastline, starting at Magdalena Bay and tracing its progress northward (Fig. 1). Magdalena Bay and adjacent Almejas Bay possess a richly developed tropical fauna, consisting for the most part of species ranging continuously to Panama and beyond. The spider crabs, families Majidae and Parthenopidae, are represented inside Magdalena Bay by no less than 24 species, with two additional in Santa Maria Bay, on the outer coast at the same latitude. (It will be remembered that it is at Pta. Entrada, outside Magdalena Bay, that the northern species, *Taliepus nuttalli, Epialtus hiltoni,* and *Pachygrapsus crassipes,* make their last stand coming south.) Of these 26 species, only six range north of Pta. Eugenio, and of these *Pitho picteti* and *Inachoides laevis* drop out at Scammon Lagoon, *Pelia tumida* drops out at San Pedro, *Erileptus spinosus* at Santa Barbara, *Podochela hemphilli* at Monterey Bay, and *Pyromaia tuberculata* continues to Monterey Bay and Tomales Bay, north of San Francisco.

The cancroid crabs, families Portunidae, Cancridae, and Xanthidae, are represented at Magdalena Bay by 10 species,

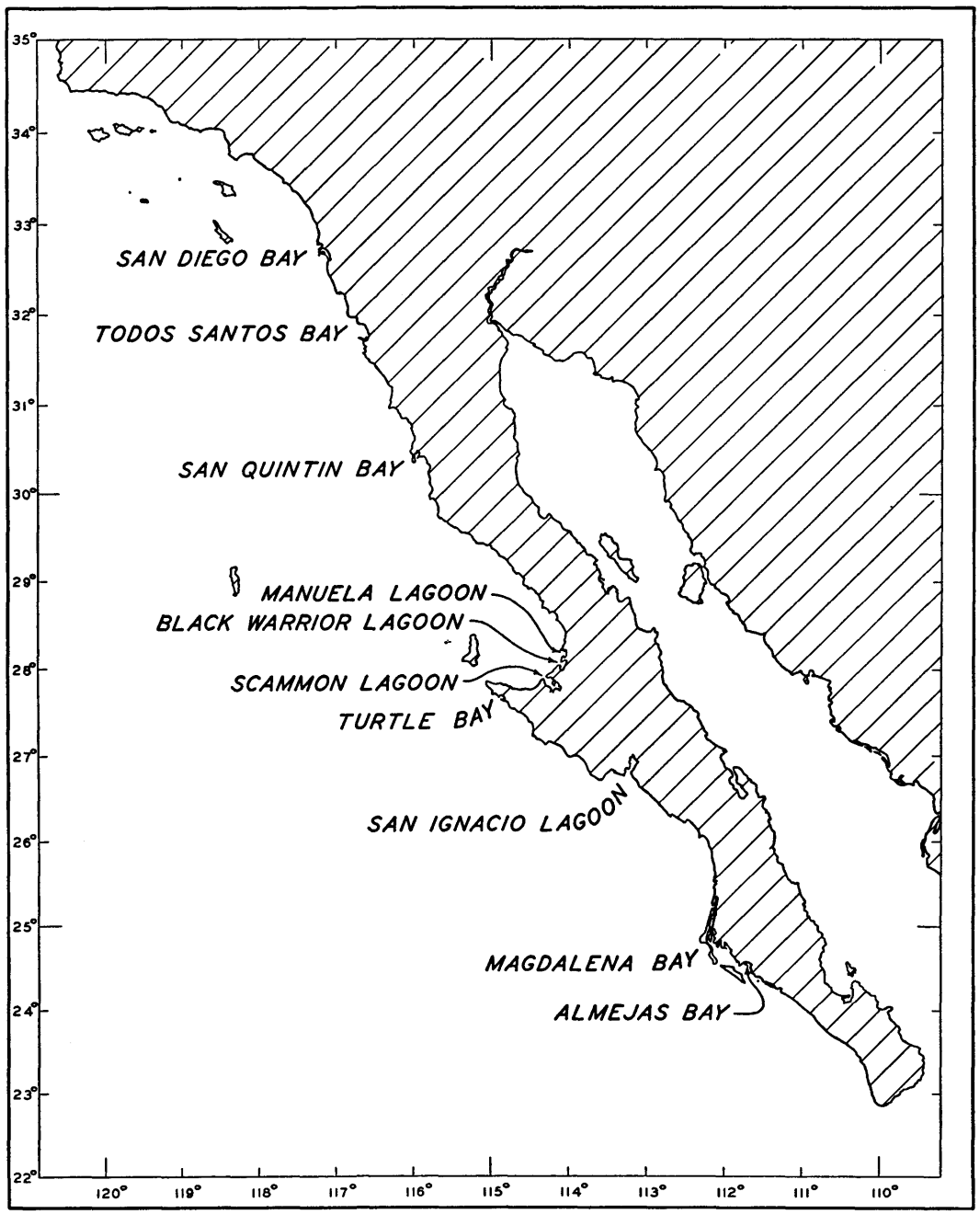

FIG. 1. The peninsula of Baja California, showing the west coast bays and lagoons that serve as refuges for warm-water relict species.

plus an additional six species in Santa María Bay, outside. Of these 16 species, 10 range farther north, and of these *Leptodius occidentalis* drops out at San Ignacio Lagoon, *Eurytium affine* at Turtle Bay, *Callinectes bellicosus* at San Diego

Bay, *Cancer amphioetus* and *Lophopanopeus frontalis* at Newport Bay, *Callinectes arcuatus* at Anaheim Bay, *Pilumnus spinohirsutus* at San Pedro, *Portunus xantusii* at Santa Barbara, *Paraxanthias taylori* at Monterey Bay, and *Cancer anthonyi* at Monterey Bay and Bodega Bay, north of San Francisco.

Of the grapsoid crabs, families Grapsidae and Ocypodidae, the mangrove crab, *Goniopsis pulchra,* makes its last stand on Mangrove Island in Magdalena Bay, where also occurs the mangrove crab, *Sesarma magdalenense.* The fiddler crab, *Uca crenulata,* occurs at Magdalena, Santa María, San Quintín, San Diego, Newport, Alamitos Bays, and Playa del Rey in estuarine situations.

It is significant that the most northerly occurrence of these tropical or semitropical species is in a protected bay or lagoon, sheltered from upwelling by a shallow sill, and with maximum insolation present, while the nearest unprotected situation in which the species is found may be several hundred miles to the southward. It is apparent that the present tropical relicts of the west coast bays and esteros may date from no earlier than the latest interglacial period. If this be true, we have in the difference in temperature between the outer coastal waters opposite the present relict location and the most northerly locality at which the species occurs in the open ocean an empirical measure of the displacement of isotherms that has occurred since the range was continuous.

Recent exploration of the Vizcaíno Bay region, and in particular, of Scammon, Black Warrior, and Manuela lagoons, by the *Velero IV,* the Kenyon-Williams, and the Knudsen-Gorsline (*Horizon*) expeditions, has yielded unexpected results, insofar as the Brachyura are concerned. From Vizcaíno Bay itself have come the spider crab, *Microphrys platysoma,* dredged at Pta. Malarrimo, and the xanthid crab, *Eurypanopeus planissimus,* collected intertidally at North Bay, Cedros Island. From Lagoon Head anchorage (Fig. 2) on seaweeds, has come the sargassum crab, *Epialtus minimus,* while from shallow dredging inside Scammon Lagoon (Fig. 3) itself have come the spider crab, *Podochela latimanus,* and the xanthid crab, *Hexapanopeus rubicundus,* which last occurs in San Quintín Bay as well. These species are unknown from the west coast of Baja California apart from these unpublished records, and have been considered Gulf of California endemic species. Moreover, the three spider crabs show a degree of differentiation from their Gulf of California counterparts, although at no more than the subspecies level. If these were widely ranging southern California-west coast of Baja California species found isolated in the upper part of the Gulf of California, we would recognize a familiar situation and know how to treat it taxonomically. They are, however, widely ranging Gulf of Cali-

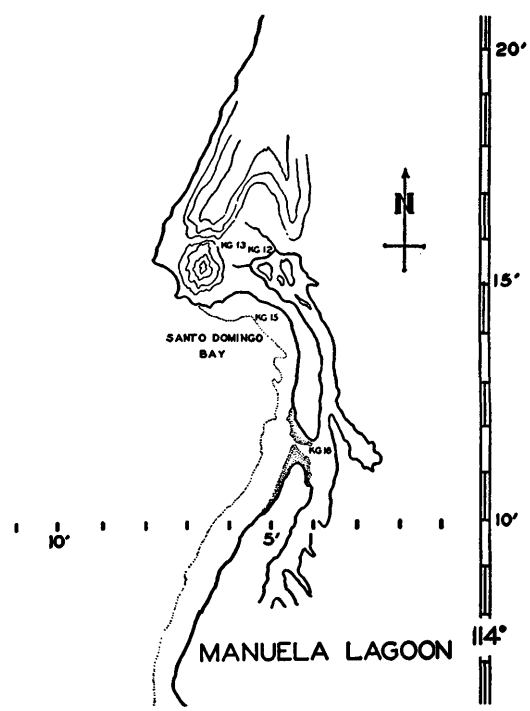

FIG. 2. Manuela Lagoon, in the Vizcaíno Bay region, showing Knudsen-Gorsline stations. The Gulf of California sargassum crab, *Epialtus minimus,* was obtained here, at 28° N. Latitude.

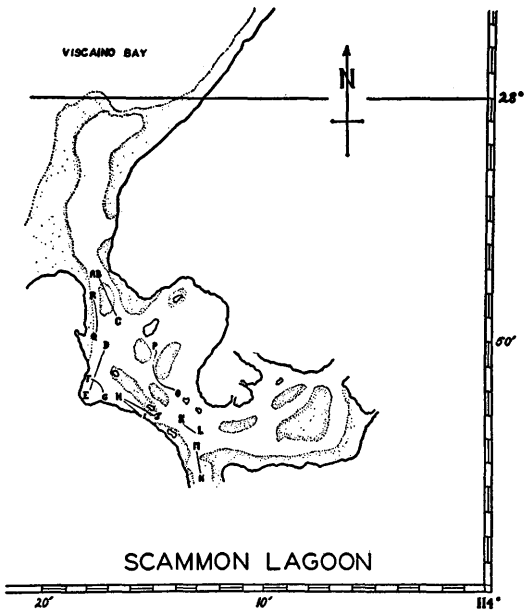

FIG. 3. Scammon Lagoon entrance from Vizcaíno Bay, showing dredge stations at which the Gulf of California species, *Podochela latimanus* and *Hexapanopeus rubicundus,* were collected.

fornia species found isolated in a few west coast lagoons. In this case the pattern of the interglacial relicts of the more northerly bays and estuaries suggests an explanation: are not these also the relicts of an earlier advance up the west coast of warm-water species for which suitable temperature conditions no longer exist on the unsheltered peninsula, but for which the temperature regime of these sheltered bays, as of the Gulf of California, remains ideal? The fact that most of them represent tropical, rather than temperate, genera lends credence to this view.

In concluding the presentation of distribution of Brachyura on the Pacific coast of Baja California, it may be stated by way of summary: (1) that the region between Pt. Conception, California, and Pta. Entrada, Baja California, constitutes a transition area between the north-temperate and tropical marine faunas; (2) that within this area cold-water species are found in progressively diminishing numbers from north to south, clinging most persistently to rocky headlands, where upwelling occurs; (3) that within this area warm-water species are found in progressively smaller numbers from south to north, frequently making their last stand in a shallow bay or estuary where insolation is present, separated by a discontinuity of tens or hundreds of miles from their next most northerly occurrence in the open ocean; and (4) that this discontinuity gives an empirical measurement of the displacement of isotherms that has occurred since the time of continuous range.

The Gulf of California

The Gulf of California presents a special problem, extending as it does well north of the latitude of Cedros Island and enclosing a body of water which at its northern end is temperate (but with high summer temperatures), while its southern end and only present communication with the Pacific lies well within the tropics. It has generally been considered as supporting a Panamic fauna only, although Hubbs (1948; 463) mentions dilution of Panamic types with California coastal types of fishes in its upper portion. Southern California-northern Baja California coastal types of Brachyura found in the Gulf of California include the following: among the oxystomes, *Hepatus lineatus* and *Randallia ornata;* among the spider crabs, *Podochela lobifrons* (formerly known as *P. barbarensis*) and *P. hemphilli, Pyromaia tuberculata,* and *Erileptus spinosus;* among the cancroid crabs, *Cancer amphioetus, Lophopanopeus frontalis,* and *Pilumnoides rotundus;* and among the grapsoid crabs, *Pachygrapsus crassipes* and *Uca crenulata.* Differentiation of the Gulf population from that of the outer coast varies from none at all in the case of *Pachygrapsus crassipes* through populational in the case of *Randallia* (where the Gulf population, described as a full species, *R. angelica,* is not

now thought to be so), to subspecific in the case of *Pyromaia* (where *P. mexicana* was removed from synonymy and established as a subspecies of *P. tuberculata*), to full species in the case of the *Libinia setosa-L. mexicana* species pair. The degree of differentiation seems to be related to the temperature tolerance of the species concerned: the eurythermic and widely ranging species are undifferentiated, the stenothermic and narrowly ranging species are most completely differentiated. This leads us to a consideration of the Gulf of California endemic species.

Among the spider crabs, family Majidae, two well-defined forms are restricted to the upper portion of the Gulf of California. One, *Libinia mexicana,* occurs from Rocky Point (Pta. Peñasco) south to San Felipe on the peninsula side and to San Ignacio Bay, Sinaloa, on the mainland side, and has as its cognate *L. setosa* of the west coast of Baja California. The other, *Pyromaia tuberculata mexicana,* occurs from Rocky Point south to Willards Point on the peninsula side and to outside Guaymas on the mainland side, and is clearly a geographical segregate of the widely ranging *P. t. tuberculata.* Other species taken at Rocky Point, or at least as far north as Puerto Refugio, Angel de la Guarda Island, range southward as follows: *Podochela latimanus* and *Epialtus minimus* to La Paz Bay (and on the west coast at Scammon Lagoon), *Stenocionops beebei* to Puerto Escondido (and at Santa María Bay), *S. angusta* (formerly known as *S. contigua*) to San Lorenzo Channel (and at Magdalena Bay), *Eucinetops lucasi* and *Collodes tumidus* to Cabeza Ballena (the latter at Magdalena Bay and east of Cedros Island). Three other species appear to be restricted to the southern portion of the Gulf: *Herbstia camptacantha* from Patos Anchorage to San Gabriel Bay, Espíritu Santo Island (extralimital at Tangola-Tangola), *Epialtus sulcirostris* from San Marcos Island to Cabeza Ballena, and *Hemus analogus* from Isla Partida to San Gabriel Bay (and Tenacatita Bay on the mainland).

The spider crabs of the family Parthenopidae have not developed Gulf of California endemic species, with the possible exception of *Parthenope triangula,* which ranges from Puerto Escondido to off Los Frailes on the peninsula side and occurs in Magdalena Bay. However, it ranges via Socorro, Clarion, and Galápagos Islands to La Plata Island, Ecuador, although it has not been collected from the mainland.

Of some 21 species of cancroid crabs of the family Xanthidae that have their center of distribution in the Gulf of California, eight, or over a third, are restricted to its northern part. These include five with extremely limited ranges centering around San Felipe: *Panopeus diversus,* known also from Cholla Bay! (! = new record); *Neopanope peterseni,* Angeles Bay! to Puerto San Carlos; *Eurypanopeus confragosus, Eurytium albidigitum,* and *Pilumnus tectus,* collected so far only at San Felipe. The other three range farther south, but in no case farther than North Bay, San Francisco Island: *Glyptoxanthus meandricus,* Punta Peñasco to San Francisco Island! and outside Guaymas!; *Eurypanopeus ovatus,* San Felipe! to Puerto Escondido! and outside Guaymas!. None of these species occur on the west coast of Baja California, insofar as is known.

Another group of eight species ranges throughout the Gulf and frequently beyond its confines. These are *Leptodius occidentalis,* San Luis Gonzales Bay to Punta Trinidad! (and on the west coast north to San Juanico Bay and San Ignacio Lagoon!), *Lophopanopeus frontalis,* Rocky Point! to La Paz (and north to Santa Monica Bay), *Eurypanopeus planissimus,* Tepoca Bay! to Punta Trinidad! (and Magdalena Bay and North Bay, Cedros Island), *Eurytium affine,* San Luis Gonzales Bay to Pichilinque Bay (and at Magdalena Bay and Turtle Bay), *Pilumnus townsendi,* Adair Bay to La Paz

(and Magdalena Bay), *Hexapanopeus rubicundus,* San Felipe to La Paz! (and at Scammon Lagoon and San Quintín Bay!), *Micropanope areolata,* Rocky Point! to Los Frailes! (and San Juanico Bay!). *Leptodius occidentalis* and *Eurytium affine* occur also as vagrants in the Galápagos Islands, but are not found on the mainland south of Manzanillo, being replaced there by Panamic species.

Another group of four species occurs in the southern portion of the Gulf only. These are *Micropanope cristimana* and *Pilumnus stimpsoni,* Cape San Lucas and Manzanillo; *Paraxanthias insculptus,* Cape San Lucas and Galápagos; and *Micropanope nitida,* Salinas Bay, Carmen Island! to La Paz Bay!.

The cancroid crabs of the family Portunidae, or swimming crabs, have two Gulf of California endemic species: *Portunus minimus,* Tiburon Island to Tres Marias Islands, and *P. pichilinquei,* Cape Tepoca to Pichilinque Bay (and Magdalena Bay on the outer coast). However, the exhaustive series in the Hancock collections suggests that these may represent but a single species.

The grapsoid crabs of the family Goneplacidae are mud dwellers and it is not surprising to find them prominent in the upper Gulf fauna. *Oediplax granulata* and *Panoplax mundata* both occur in the vicinity of Consag Rock, while *Trizocarcinus dentatus* is found from Pta. San Fermin to Cape Lobos, and also at Espíritu Santo Island. Of these only *Oediplax granulata* occurs on the west coast of Baja California, at Pta. Tosco. *Chasmocarcinus ferrugineus,* described from Pta. Arena, is believed to be synonymous with the Panamic *C. latipes.* (See Garth, 1940.)

The grapsoid crabs of the family Pinnotheridae are commensals found in association with mollusks, annelids, and echinoderms. The 18 species occurring in the Gulf of California as endemics reflect the indefatigable efforts of the late S. A. Glassell; their "distribution" is the pattern of his collecting localities. Of this number 10 have been collected only at San Felipe and/or Rocky Point and must tentatively be classified as upper Gulf species. Three more, known only from San Felipe or Rocky Point in the Gulf but occurring also at Magdalena Bay, suggest a wider Gulf of California distribution. Two, known only from Pichilinque Bay, are tentatively considered southern; one known only from Mulegé Bay might be either northern or southern. The ranges of their commensal hosts will define their ultimate distribution.

The grapsoid crabs of the family Cymopoliidae yield two endemic species of general distribution: *Cymopolia zacae,* Puerto Refugio to Cape Pulmo, and *C. zonata,* Puerto Refugio to Cabeza Ballena on the peninsular side, Tiburon Island to Ensenada de San Francisco, outside Guaymas, on the mainland side (and at Magdalena Bay on the west coast). A third species, *C. cortezi,* described from Puerto Escondido, has been collected at Wenman Island in the Galápagos. Like the Goneplacidae, the Cymopoliidae are dredged.

The grapsoid crabs of the family Grapsidae have two Gulf endemics, *Cyclograpsus escondidensis,* Gonzaga Bay to Puerto Escondido, and *Goetice americanus,* [San Luis] Gonzales Bay to Georges Island (and at San Bartolomé Bay on the outer coast). *Sesarma magdalenense* is a Magdalena Bay endemic, occurring there on mangrove trees.

The grapsoid crabs of the family Ocypodidae have two Gulf endemics, *Uca coloradensis* and *U. monilifera,* both confined to the mouth of the Colorado River.

Although perhaps of greater interest from an evolutionary and distributional standpoint, it is neither the Gulf of California endemics nor the southern California-northern Baja California coastal types that predominate throughout most of the Gulf, but the vastly greater array of species that have invaded the region from the American tropics, many of

which range continuously to Panama and beyond. In an attempt to define the distribution of Panamic species in the Gulf of California, the advance of each up both the mainland and peninsular east coast was traced; the endpoints were established from Hancock expeditions records, supplemented by published records of other expeditions. Since the data are voluminous, they are presented in a series of tables that include, for purposes of comparison, the advance of these species up the peninsular west coast as well. A résumé by families is here given:

Of the spider crabs of the family Majidae (Table I) 37 Panamic species are present, 32 of them on the mainland side and 31 of them on the peninsular side of the Gulf of California, with 12 on the peninsular west coast. Of these 37 species, 19, or more than half, are present north of a line drawn from San Francisco Point to the south end of Tiburon Island, where the Gulf conspicuously narrows. Of the 12 species that reach Puerto Refugio, Angel de la Guarda Island, 11 are normally dredged, while the single shore species, *Ala cornuta,* continues with three dredged species to Rocky Point. This suggests that the Panamic shore species are first to drop out; however, it should be borne in mind that the greater tidal amplitudes of the upper Gulf tend to obscure the usually sharp demarcation between intertidal and subtidal zones.

Of the spider crabs of the family Parthenopidae (Table I) 11 Panamic species are present, eight on the mainland side and nine on the peninsular side of the Gulf of California, with six on the peninsular west coast. Of these 11 species, six, or over half, attain a line drawn from San Marcos Island diagonally northward to Guaymas, somewhat south of the narrows. The family is a tropical one, with but one north-temperate species, *Heterocrypta occidentalis,* on the west coast.

Of the cancroid crabs of the family Portunidae (Table II) 11 Panamic species are present, 10 on the mainland side, six on the peninsular east side, and five on the peninsular west side. Of these 11 species, four come no farther north than Isabel Island or Punta Piaxtla (Mazatlán), but only one of them crosses the Gulf to Los Frailes. Only four of the 11 are present at Guaymas, and of these *Arenaeus mexicanus* continues to Tepoca Bay on the east side and *Callinectes bellicosus* to San Felipe on the west side of the Gulf, reflecting the difference in their ecological preferences, the former for open sandy beaches, the latter for protected lagoons.

Of the cancroid crabs of the family Xanthidae (Table II) 33 Panamic species are present, 27 on the mainland side and 29 on the peninsular side of the Gulf of California, with 12 on the peninsular west coast. Of the 27 from the mainland side, 13, or nearly half, are unrecorded from north of Isabel Island or Tres Marías Islands; however, peninsular records are available for 12 of the 13, possibly because the mainland coast between Banderas Bay and Guaymas has been insufficiently collected. While this is true enough, another explanation seems plausible. When the ecology of these 13 xanthid species is considered, it is found that eight of them inhabit the *Pocillopora* coral colony exclusively, while at least three more are frequently encountered in this habitat. Could it not be that the heavy surf that precludes landing along this unprotected, sandy coast has produced conditions that are unfavorable for the establishment of stony corals also?

Of the 29 species represented on the peninsular side, 16, or more than half, are still present at Puerto Escondido. Seven species occur from San Marcos Island north, of which one, *Eriphia squamata,* persists in the intertidal zone to San Felipe and to Rocky Point. The family is highly developed in the tropics and includes a large proportion of the coral commensals. With the exception of *Carpilodes cinctimanus,* taken recently at Puerto Escondido, these come no farther north than Espíritu Santo Island.

Of the grapsoid crabs of the family

TABLE I—PANAMIC SPECIES OF MAJOIDEA OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
MAJIDAE				
Eucinetops panamensis		Angel de la Guarda I.	Tiburon Island	S
Euprognatha bifida	San Benito Islands	Angel de la Guarda I.	Tepoca Bay	D
Collodes granosus		Los Frailes	Pta. Piaxtla	D
Collodes tenuirostris	Cedros Island	Puerto Refugio	Tepoca Bay	D
Paradasygyius depressus		Concepción Bay	Ensenada de San Francisco	D
Pyromaia t. tuberculata	(Tomales Bay)	Puerto Refugio	Tiburon Island	S–D
Inachoides laevis	Cedros Island	Puerto Refugio	Rocky Point	D
Podochela vestita	Santa María Bay	Angel de la Guarda I.	Rocky Point	D
Podochela veleronis		Los Frailes	Isabel Island	D
Stenorynchus debilis		Consag Rock	Tepoca Bay	S–D
Pitho sexdentata		Pta. Marcial Reef	Tiburon Island	S–D
Pitho picteti	Scammon Lagoon	Concepción Bay	Tepoca Bay	S–D
Tyche lamellifrons		Agua Verde Bay	Isabel Island	S–D
Sphenocarcinus agassizi		Puerto Refugio	San Pedro Nolasco	D
Acanthonyx petiverii	Santa María Bay	La Paz Bay	Mazatlán	S–D
Eupleurodon trifurcatus		Cabeza Ballena	(Acapulco)	S
Notolopas lamellatus			Rocky Point	S–D
Notolopas mexicanus			Pta. Piaxtla	S–D
Neodoclea boneti			Macapule	D
Lissa tuberosa	Magdalena Bay	Tortuga Island	Tres Marías	D
Lissa aurivilliusi	Santa María Bay	Puerto Refugio	(Tenacatita)	D
Ala cornuta		Puerto Refugio	Cholla Bay	S–D
Mithrax tuberculatus		Carmen Island	Tres Marías	S–D
Mithrax armatus		Los Frailes	Mazatlán	S
Mithrax sinensis		Puerto Refugio	San Esteban	S–D
Mithrax pygmaeus			Isabel Island	S–D
Mithrax spinipes		Agua Verde Bay		S–D
Mithrax denticulatus		Agua Verde Bay	Isabel Island	S
Teleophrys cristulipes	Santa María Bay	Agua Verde Bay	Isabel Island	S–D
Microphrys platysoma	Malarrimo Point	Puerto Refugio	Tiburon Island	S–D
Microphrys triangulatus		Concepción Bay	Isabel Island	S–D
Microphrys branchialis	Dewey Channel	Angeles Bay	Isabel Island	D
Stenocionops ovata			Tiburon Island	D
Macrocoeloma villosum		Agua Verde Bay		S–D
Macrocoeloma maccullochae			Isabel Island	D
Hemus finneganae		Puerto Refugio		S–D
Thoe s. sulcata		Puerto Refugio	Tiburon Island	S–D
PARTHENOPIDAE				
Parthenope exilipes		Boca de la Trinidad		D
Parthenope depressiuscula			Isabel Island	D
Parthenope triangula	Magdalena Bay	Puerto Escondido		D
Parthenope excavata		Puerto Refugio	Isabel Island	D
Parthenope stimpsoni			Isabel Island	D
Thyrolambrus glasselli	Magdalena Bay	San Marcos Island	(Tenacatita)	D
Solenolambrus arcuatus		Los Frailes	Tepoca Bay	D
Leiolambrus punctatissimus	Point Tosco	Cabeza Ballena	Off San Blas	D
Mesorhoea belli	San Juanico Bay	Puerto Refugio	Georges Island	D
Cryptopodia hassleri	Santa María Bay	Puerto Refugio	Ensenada de San Francisco	D
Heterocrypta macrobrachia	Santa María Bay	Consag Rock	Rocky Point	D

S = shore-collected D = dredged

TABLE II—PANAMIC SPECIES OF CANCROIDEA OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
PORTUNIDAE				
Portunus acuminatus			Isabel Island	D
Portunus asper			Pta. Piaxtla	D
Portunus affinis			Isabel Island	D
Portunus tuberculatus		Los Frailes	Isabel Island	D
Portunus iridescens	Santa María Bay	Santa Inez Bay	San Ignacio Bay	D
Callinectes bellicosus	Scammon Lagoon	San Felipe	Puerto San Carlos	S–D
Callinectes arcuatus	Manuela Lagoon	Espíritu Santo I.	Guaymas	S–D
Callinectes toxotes		Cape San Lucas		S–D
Arenaeus mexicanus	Santa María Bay	Puerto Escondido	Tepoca Bay	D
Cronius ruber	Cedros Island		Guaymas	S–D
Euphylax robustus			Yavaros	
ATELECYCLIDAE				
Pliosoma parvifrons	Santa María Bay	Los Frailes		D
Kraussia americana		Puerto Refugio		D
CANCRIDAE				
Cancer porteri			Rio San Lorenzo	D
XANTHIDAE				
**Carpilodes cinctimanus*		Puerto Escondido	Isabel Island	S
Platypodia rotundata	Santa María Bay	Salinas Bay	Bahía Catalina	S
Actaea dovii		San Francisco I.		S
Actaea sulcata		Espíritu Santo I.	Tiburon Island	S–D
Lipaesthesius leeanus		San José Island	Tiburon Island	D
Medaeus lobipes	Santa María Bay	Cape Pulmo	San Ignacio Bay	D
**Medaeus spinulifer*		Fraile Bay		S–D
Medaeus pelagicus	Magdalena Bay	Consag Rock	San Pedro Nolasco	D
**Daira americana*		Carmen Island	Isabel Island	S–D
Cycloxanthops vittatus		Carmen Island	Puerto San Carlos	S–D
Xanthodius sternberghii	Magdalena Bay	Willard Point	George Island	S
Xanthodius stimpsoni		Espíritu Santo I.	Tres Marías Ids.	S–D
Lophoxanthus lamellipes		Puerto Escondido	Tres Marías Ids.	S–D
Hexapanopeus orcutti			Topolobampo	S–D
Hexapanopeus sinaloensis	Santa María Bay			D
Lophopanopeus maculatus		San Marcos Island		D
Panopeus chilensis			Guaymas	S
Panopeus purpureus	Cedros Island	San Felipe		S
Panopeus bermudensis	San Ignacio Lagoon	Puerto Escondido	Guaymas	D–S
**Micropanope xantusii*		Partida Island	Isabel Island	S–D
Micropanope polita	Guadalupe Island	Puerto Refugio	Tiburon Island	D
Micropanope lata	San Jaime Bank		San Pedro Nolasco	D
Micropanope armstrongi	Santa María Bay			D
Pilumnus limosus		Gonzaga Bay	Tiburon Island	S
Pilumnus pygmaeus	Santa María Bay	San Marcos Island	Isabel Island	S–D
Pilumnus stimpsoni		Los Frailes		D
**Heteractaea lunata*		Agua Verde Bay	Isabel Island	S–D
Heteractaea peterseni		San Francisco I.		D
Ozius verreauxii			Isabel Island	S
Ozius perlatus		Cabeza Ballena	Isabel Island	S
Epixanthus tenuidactylus		Concepción Bay	Isabel Island	S–D
Eriphia squamata	San Juanico Bay	San Felipe	Cholla Bay	S
**Domecia hispida*		Espíritu Santo I.	Isabel Island	S–D
**Trapezia cymodoce ferruginea*		Espíritu Santo I.	Isabel Island	S–D
**Trapezia digitalis*		Espíritu Santo I.	Isabel Island	S–D

* Inhabitant of the *Pocillopora* coral colony.

Goneplacidae (Table III) eight Panamic species are present, four on the mainland side, five on the peninsular east coast, and five on the peninsular west coast. Of the eight species, two barely enter the Gulf of California, one reaches Angel de la Guarda Island, while four persist to San Felipe, Consag Rock, or Rocky Point.

Of the grapsoid crabs of the family Pinnotheridae (Table III) six Panamic species are present, two on the mainland side, three on the peninsular east coast, and one on the peninsular west coast. Of these *Pinnixa transversalis,* commensal in worm tubes, is most persistent, continuing to San Felipe and Rocky Point.

Of the grapsoid crabs of the family Cymopoliidae (Table III) two Panamic species occur in the Gulf. Of these *Cymopolia fragilis* is more widely distributed, occurring on all three coasts, while *C. lucasii* appears limited to the peninsular east coast.

Of the grapsoid crabs of the family Grapsidae (Table III) nine Panamic species are present, five on the mainland coast, eight on the peninsular east coast, and five on the peninsular west coast. Of the eight species, three barely enter the Gulf at Isabel Island or Cape San Lucas, one reaches Concepción Bay, while two persist to Guaymas and beyond. Best known and most conspicuous, *Grapsus grapsus* was found by Hancock Expeditions north to San Esteban Island, in the aforementioned narrows. [As "Sally Lightfoot" it is mentioned as occurring at Puerto Refugio by Steinbeck and Ricketts (1941; 225), albeit in the narrative rather than in the systematic section.] Although found north to Cedros Island on the peninsular west coast, *Pachygrapsus transversus* comes no farther north than Espíritu Santo Island on the peninsular east coast. The mangrove crab, *Goniopsis pulchra,* drops out at Espíritu Santo Island and at Magdalena Bay, on the east and west peninsular coasts, respectively, but occurs at Guaymas on the mainland.

Of the grapsoid crabs of the family Gecarcinidae (Table III), the land crabs, *Gecarcinus planatus* comes north to San Ignacio Bay, Sinaloa, *Ucides occidentalis* to Espíritu Santo Island, and *Cardisoma crassum* to Agua Verde Bay. None of these occurs on the west side of Baja California, insofar as is known.

Of the grapsoid crabs of the family Ocypodidae (Table III), the ghost crab, *Ocypode occidentalis,* is found on sandy beaches at Agiabampo on the mainland, at Carmen Island on the peninsular east coast, and north to Todos Santos Bay on the peninsular west coast. Of seven Panamic species of fiddler crabs, genus *Uca,* three occur on the mainland north to Guaymas and vicinity, four on the peninsular east coast, of which one reaches Carmen Island, and three on the peninsular west coast, of which one reaches San Bartolomé Bay.

In conclusion, it may be stated that the northern limit of the Panamic fauna in the Gulf of California cannot presently be defined because the dropping out of tropical species is gradual and occurs throughout its entire length, with 50% of the Panamic species still present in its upper portion. It is also apparent that the region immediately north of the narrows has the greatest rate of species change.

Insular Species

In an earlier paper (Garth, 1946) attention was called to the 11 species of Brachyura common to the Gulf of California and the Galápagos Islands, but not found along the mainland from the Gulf of California to Ecuador. Such species, comprising 9% of the Galápagos brachyuran fauna, were believed to have been transported in the larval stage by the southerly directed California current and the eastwardly directed Equatorial counter current. Significantly, they represent a larger fraction of the Galápagos brachyuran fauna than the five species, or 4%, common to the Galápagos Islands

TABLE III—PANAMIC SPECIES OF GRAPSOIDEA OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
GONEPLACIDAE				
Chasmocarcinus latipes	Cedros Island	Angel de la Guarda		D
Chasmophora macrophthalma	Point Tosco	Gorda Point		D
Cyrtoplax panamensis		San Felipe	Isabel Island	D
Euryplax polita			Isabel Island	S–D
Glyptoplax pugnax				
Prionoplax ciliata	Point Tosco			D
Speocarcinus californiensis	(Mugu Lagoon)	Gonzaga Bay	Rocky Point	S–D
Speocarcinus granulimanus	Cedros Island	Consag Rock	Rocky Point	D
PINNOTHERIDAE				
Dissodactylus nitidus	Abreojos Point	Concepción Bay		S
Pinnixa affinis				
Pinnixa transversalis		San Felipe	Rocky Point	D
Pinnotheres lithodomi				
Pinnotheres margarita		Mulegé Bay		S
Pinnotheres orcutti			Tres Marías Ids.	
CYMOPOLIIDAE				
Cymopolia fragilis	Cedros Island	Inner Gorda Bank	Guaymas	D
Cymopolia lucasii		Angel de la Guarda		D
GRAPSIDAE				
Aratus pisonii	Magdalena Bay		Isabel Island	S
Geograpsus lividus		San Francisquito	Santa Barbara	S
Goniopsis pulchra	Magdalena Bay	Espíritu Santo I.	Guaymas	S
Grapsus grapsus	San Benito Ids.	Puerto Refugio	Tiburon Island	S
Pachygrapsus transversus	Cedros Island	Espíritu Santo I.	Isabel Island	S
Percnon gibbesi		Cape San Lucas		S
Plagusia depressa tuberculata		Cape San Lucas		
Planes cyaneus	(San Francisco)	Santa Inez Bay	Escuinapa	
Sesarma sulcatum		Concepción Bay		S
GECARCINIDAE				
Cardisoma crassum		Agua Verde Bay		S
Gecarcinus planatus			San Ignacio Bay	S
Ucides occidentalis		Espíritu Santo I.		S
OCYPODIDAE				
Ocypode occidentalis	Todos Santos Bay	Carmen Island	Agiabampo	S
Uca brevifrons		Pichilinque Bay		S
Uca macrodactyla			Guaymas	S
Uca latimanus		La Paz		S
Uca mordax				
Uca musica	Santa María Bay	Pichilinque Bay	Tepoca Bay	S
Uca princeps	San Bartolomé Bay	Carmen Island	Ensenada de San Francisco	S
Uca reticulata	"West coast L.C."			

and Peru, for which transport by the Humboldt or Peruvian coastal current was postulated.

When it is considered that the tip of the peninsula of Baja California is effectively isolated from the opposite mainland by

deep water, and that there is no approach in the littoral for Panamic species except through the upper Gulf of California, which effectively filters them out, it is seen that for warm-water, littoral species the Cape San Lucas region is an island, and like all islands, subject to random arrival and dispersal. And just as there are brachyuran species common to Clarion and Galápagos (*Ebalia hancocki*), Clarion and Cocos (*Portunus brevimanus*), so should we expect to find species common to insular Cape San Lucas (as distinguished from the Gulf of California in its predominantly Panamic relationship) and these island outposts.

Once this is understood, the finding of the supposed Galápagos endemic *Leptodius cooksoni* first at Clarion Island, and more recently, in isolated colonies along the peninsular Gulf coast as far north as Puerto Escondido, becomes less surprising, while the range of *Parthenope triangula,* Cape region from Magdalena Bay to Puerto Escondido, Socorro, Clarion, and Galápagos Islands, and finally, La Plata Island, Ecuador, fits a pattern of random dispersal of the insular type. Furthermore, the fact that the 11 brachyuran species common to the Cape San Lucas region and the Galápagos Islands have no Atlantic analogues is a strong indication that they have never occurred in the Bay of Panama.

Summary

In the study just completed, Panamanian species intruding into the Gulf of California region (including (Magdalena Bay) numbered 131: cancroid crabs 47, grapsoid crabs 36, spider crabs 48. Species indigenous to the Gulf of California numbered 80: cancroid crabs 23, grapsoid crabs 32, spider crabs 25. Northern species numbered only 19: cancroid crabs 6, grapsoid crabs 5, spider crabs 8. To recapitulate, of a total of 230 species (cancroid crabs 76, grapsoid crabs 73, spider crabs 81), 131 species, or 57%, were Panamanian, 80 species, or 35%, were indigenous, and 19, or 8%, were northern.

When the above summary (see also Table IV) is compared with that of Glassell (1934), made just 25 years ago, it will be noted that the Panamanian segment has increased from 48 to 57% of the total, and that this has been at the expense of the indigenous element, which has declined from 40 to 34% of the total, and of the northern element, which has declined from 12 to 8% of the total. If the oxystomatous and allied crabs (Table V), 40 in number: 32 Panamic, 6 Gulf endemic, and 2 northern, omitted in order to make the above compilation more directly comparable to Glassell's, be included, the percentages become even more disparate: Panamanian 60%, indigenous 32%, northern 8%.

Further reflection reveals that the increment in the Panamanian sector has resulted, not so much from work done in the Gulf of California extending the range of Panamic species northward, as from work done in the Bay of Panama extending southward the range of species earlier known only from the Gulf of California. The smaller absolute number, as well as the lesser percentage, of northern species results in part from our inability to locate published records of their occurrence at Magdalena Bay or in the Gulf of California, presumably because these were known only to Glassell.

Conclusion

In concluding the presentation of distribution of Brachyura in the Gulf of California, it may be stated: (1) that the northern limit of the Panamic fauna in the Gulf of California cannot presently be defined because the dropping out of Panamic species is gradual and occurs throughout its entire length, with 50% of the Panamic species still present in its upper third; (2) that the southern limits of the warm-temperate fauna (the so-called "cold-water" species) may be defined by the ranges of the Gulf of California endemics

TABLE IV—A SUMMARY OF THE TOTAL NUMBER OF SPECIES IN THE THREE GROUPS

Cancroid crabs reported from Gulf of California	76 species
Grapsoid	73
Spider	81
Total of all species reported	230

The intrusion of Panamic species into the Gulf of California numbers 131 or 57% of the total. They are divided as follows:

Cancroid crabs	47 species, or	62%
Grapsoid crabs	36 ,	49
Spider crabs	48 ,	59
Total of the three groups	131 ,	57

(The above percentages represent the per cent which the Panamanian species bear to the total number of species in each family group.)

The number and percentages of species indigenous to the Gulf of California:

Cancroid crabs	23 species, or	30%
Grapsoid crabs	32 ,	42
Spider crabs	25 ,	31
Total of the three groups	80 ,	34

Northern intrusion of species in the Gulf of California:

Cancroid crabs	6 species, or	8%
Grapsoid crabs	5 ,	8
Spider crabs	8 ,	10
Total of the three groups	19 ,	8

A recapitulation of the foregoing tables:

Panamanian species in the Gulf	131 species, or	57%
Indigenous species	80 , or	35
Northern species	19 , or	8
	250 ,	100

and the southern California-northern Baja California coastal types occurring in the upper portion of the Gulf; and (3) that the Cape San Lucas "insular" region (Magdalena Bay to Puerto Escondido) supports a warm-water littoral fauna that is shared with the offshore islands of Socorro, Clarion, and Galápagos, and is independent of the mainland Panamic fauna of the Gulf.

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Addendum

The Scripps Institution of Oceanography Vermilion Sea Expedition with Robert H. Parker in charge of the biological phases of the investigation collected from 103 stations off Baja California and in the Gulf of California, March 2–May 20, 1959. Although ranging north of Angel de la Guarda Island, its chief contribution to faunistic studies was in the southeastern part of the Gulf, where a number of stations were occupied within the 100-fathom contour along the continental shelf, several to 800 fathoms on the continental slope, and one abyssal station in 1640 fathoms northwest of Tres Marias Islands. Only one brachyuran new to the Gulf fauna, *Ethusina faxonii,* resulted from the deeper haul, but new Gulf records may be reported for *Ethusina ciliatifrons* off Río San Lorenzo, 42–48 fathoms, *Mursia gaudichaudii* off Robelar, 48 fathoms, *Leiolambrus punctatissimus* off San Blas, 26 fathoms, *Cancer porteri* off Río San Lorenzo, 59–70 fathoms, and *Oediplax granulata* off Pta. Piaxtla, 24–26 fathoms. With the exception of the last, which is a Gulf of California endemic species with range extension southward, all are Panamic species with range extension northward.

TABLE V—PANAMIC SPECIES OF OXYSTOMATA AND ALLIED CRABS OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
RANINIDAE				
Raninoides benedicti		Willard Point		D
Raninoides ecuadorensis		Puerto Refugio		D
Ranilia fornicata	Santa María Bay	Carmen Island		D
DROMIIDAE				
Dromidia larraburei	(Monterey Bay)	Consag Rock	Rocky Point	S–D
Hypoconcha panamensis		Puerto Refugio	Rocky Point	D
Hypoconcha lowei		San Felipe	Rocky Point	D
Hypoconcha californiensis		San José Island		D
DYNOMENIDAE				
Dynomene ursula		Espíritu Santo I.	Tres Marías Ids.	S–D
DORIPPIDAE				
Ethusa mascarone americana		Consag Rock	Rocky Point	D
Ethusa mascarone panamensis			Isabel Island	S–D
Ethusa lata	San Roque Island	San Felipe	Tepoca Bay	D
Ethusa ciliatifrons			Río San Lorenzo	D
LEUCOSIIDAE				
Ebalia magdalenensis	Scammon Lagoon	Concepción Bay	Rocky Point	D
Lithadia cumingii	Magdalena Bay	Puerto Refugio	Georges Island	D
Speloeophorus digueti		Puerto Refugio	Rocky Point	D
Uhlias ellipticus		San José Island		S
Persephona edwardsii	Santa María Bay		Punta Piaxtla	D
Persephona subovata	Abreojos Point	Angel de la Guarda	Tiburon Island	D
Persephona townsendi		San Fermin Point	Cape Lobos	D
Leucosilia jurinei			Mazatlán	S
Randallia bulligera	San Diego	San José del Cabo	San Ignacio Bay	D
Randallia agaricias	Thurloe Bay	Cape San Lucas	Tres Marias Ids.	D
Iliacantha hancocki	Santa María Bay		San Ignacio Bay	D
Iliacantha schmitti	Point Tosco	Angel de la Guarda	San Pedro Nolasco	D
CALAPPIDAE				
Calappa convexa	Magdalena Bay	San Francisquito Bay	Rocky Point	S–D
Calappa saussurei	Point Tosco	Puerto Refugio	Ensenada de San Francisco	D
Mursia gaudichaudii	Farallones	Inner Gorda Bank	Off Robelar, Sin.	D
Cycloes bairdii	Santa María Bay	Los Frailes	Isabel Island	D
Hepatus kossmanni	Abreojos Point	Angeles Bay	Tiburon Island	D
Hepatella amica			Isabel Island	D
Osachila levis		Puerto Refugio	San Pedro Nolasco	D
Osachila lata			Tres Marías Ids.	D
HAPALOCARCINIDAE				
Hapalocarcinus marsupialis		Espíritu Santo I.		S

Cancer porteri may now be reported as a bi-temperate species that transgresses the tropics by submergence, being found in the Gulf of California, the Bay of Panama in 210 to 286 fathoms, and from Peru to Chile in the sublittoral.

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The Distribution and Affinities of the Marine Fish Fauna of the Gulf of California

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ALTHOUGH the fish fauna of the Gulf of California is clearly part of the Panamic fauna of the Eastern Tropical Pacific Region, it has certain peculiarities and distinctive elements which mark it with a character of its own. Beyond this, there are several areas within the Gulf with unique faunal peculiarities, which seem to have arisen in response to ecological factors. Although these areas are definitely different one from the other, they are not necessarily sharply delimited, and we know nothing about possible shifts in their ranges from year to year. It seems wiser at this time to treat them as areas with more or less distinct faunal assemblages, without attempting any sort of zoogeographic classification along a hierarchic system.

The region covered by this paper includes the entire Gulf of California, bounded on the south by Cabo San Lucas on the Baja California side, and by Topolobampo on the eastern or mainland side. Relatively little has been published on the fishes of this area. Most of the literature consists of lists of fishes collected at restricted localities and of descriptions of new species. Two checklists covering this region have appeared, but they were both merely uncritical literature compilations. The most valuable contributions have come from several recent group revisions (Briggs, 1955; Hubbs, 1952; Rosenblatt, 1959; and Springer, 1958). These papers have cleared up the problems of relationships in previously poorly understood groups, and the authors have discussed the zoogeographic implications of their findings. Unfortunately, all of the groups recently revised have consisted of fishes of rocky shores and of relatively shallow water. The authors reach reasonably uniform conclusions, but generalization on fish distribution cannot be attempted without consideration of the fishes from other habitats.

Even though literature records are scanty, there is a great amount of information available on the Gulf of California region in the form of as yet unreported, or only partially reported, collections. At the University of California, Los Angeles, we have 441 collections of fishes, comprising many thousands of specimens, from this area. This paper is largely based on these materials, and on the information gained on expeditions